

Personality Traits in Dumpling Squid (*Euprymna tasmanica*): Context-Specific Traits and Their Correlation With Biological Characteristics

David L. Sinn and Natalie A. Moltschaniwskyj
University of Tasmania

Personality traits are a major class of behavioral variation often observed within populations of animals. However, little is known of the integration between personality and an individual's underlying biology. To address this, the authors measured personality traits in squid (*Euprymna tasmanica*) in 2 contexts while also describing trait correlates with biological parameters. Four traits (*shy avoidance–bold aggression*, *activity*, *bury persistence*, and *reactivity*) were reliably measured; however, trait expression between contexts was not correlated and thus was context-specific. Trait variation was not a function of gender or of somatic or reproductive condition but was explained partially by a squid's sexual maturity and its size. Results are discussed in terms of the interplay between personality variation and resulting life history strategies in animals.

Variation in behavioral phenotypes, maintained by natural selection on individuals (Sober, 1984; Sober & Lewontin, 1982), is frequently observed in wild populations of animals. This individual behavioral variation normally involves either discrete (qualitative) or continuous (quantitative) trait expression. It is evident that individual differences in discrete behavioral traits, such as polymorphic mating strategies (Brooks & Endler, 2001; Taborsky, 1994) and nonplastic behavioral "states" (e.g., *rovers* and *sitters* in fruit flies; de Belle & Sokolowski, 1987), play a role in shaping population demographics through time. However, less is known about the relationship between continuous behavioral variation, population dynamics, and life history parameters (Wilson, 1998).

Personality traits are an example of continuous intraspecific behavioral variation and describe individuals' consistent behavioral styles, as opposed to their discrete behavioral acts (Goldsmith et al., 1987; Rothbart, Ahadi, & Evans, 2000). In nonhuman animals, personality trait constructs can be invoked to meaningfully summarize aggregate behavior and to describe an individual's tendency to behave in a particular way (D. M. Buss & Craik,

1983). A number of major axes of variation, including *activity*, *shy–bold*, *reactivity*, and *aggressive* measures, continue to be identified in nonhuman animals across a wide range of taxa in a number of contexts (for reviews, see Gosling, 2001; Gosling & John, 1999). For example, bolder animals tend to show a greater propensity to take risks than do shyer ones, and more active individuals undertake more movements, in both frequency and duration, than do their less active counterparts. The reactivity continuum quantifies differences in the magnitude of response between individuals and can be a reflection of internal arousal states (Stifter & Fox, 1990). Finally, aggression measures describe how often and to what extent individuals display agonistic or attacking behaviors. Although the range of taxa studied previously highlights the importance and widespread occurrence of personality traits among animals, there is still a lack of studies concerning invertebrates, despite the high degree of behavioral (Barnes, 1987) and neural (Corning, Dyal, & Lahue, 1976) complexity in this group.

Context-specific versus domain-general expression of personality traits has recently received greater attention in human (Kagan, 2003) and nonhuman (Coleman & Wilson, 1998) studies. Personality traits are considered domain-general if expression levels of a trait are similar for an individual across a range of contexts. Domain-general can indicate that similar selective regimes are operating across the examined contexts or that mechanistic constraints are limiting the expression of context-specific behavioral optima (Sih, Bell, & Johnson, 2004). Conversely, context-specificity occurs when an individual's expression levels of a trait vary depending on the context. Context-specific trait structure highlights the importance of situation-specific selective regimes (Coleman & Wilson, 1998). For nonhuman animals, both domain-general (Capitanio, 1999; Huntingford, 1982; Lyons, Price, & Moberg, 1988; Tulley & Huntingford, 1988) and context-specific (Coleman & Wilson, 1998; Reale, Gallant, LeBlanc, & Festa-Bianchet, 2000) personality traits have been reported. Among octopuses, close relations to squid, two studies have described

David L. Sinn, School of Aquaculture and School of Plant Science, University of Tasmania, Hobart, Tasmania, Australia; Natalie A. Moltschaniwskyj, School of Aquaculture, University of Tasmania.

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Correspondence concerning this article should be addressed to David L. Sinn, University of Tasmania, Schools of Aquaculture and Plant Science, Private Bag 55, Hobart, Tasmania 7001, Australia. E-mail: david.sinn@utas.edu.au

domain-general traits (Mather & Anderson, 1993; Sinn, Perrin, Mather, & Anderson, 2001), but neither explicitly tested for context-specificity.

Psychological and biological processes occur together within an organism, and an individual's biology or personality will reflect the dynamic interplay between behavioral expression, physiologic and neural makeup, and associated feedback systems (Kagan, Reznick, & Snidman, 1988). Understanding the integration of biological and personality processes is central to understanding the relationship between continuous behavioral variation and life history strategies in animals. For example, personality expression by gender (e.g., Budaev, 1999) and maturity stage (e.g., Mathisen, Landa, Anderson, & Fox, 2003; Rochette, Tetreault, & Himmelman, 2001) may be informative of life history strategies (i.e., sex-specific reproductive effort) tied to gender-specific behavioral strategies (Magurran & Garcia, 2000). Furthermore, growth and body size of animals may be linked to personality trait expression. Growth of some schooling fishes appears to be correlated with boldness measures (Ward, Thomas, Hart, & Krause, 2004), but boldness does not appear to be a direct result of RNA levels and thus growth rate (Sundström, Petersson, Höjesjö, Johnsson, & Järvi, 2004). Instead, bold behavior in brown trout predicts dominance in feeding hierarchies, thus indicating the importance of behavior (boldness) in determining biological outcomes (growth rate). Two other biological parameters, somatic and reproductive condition, may also be linked to phenotypic selection in animals (Hoey & McCormick, 2004). Activity measures can reflect the interplay between metabolic demand, energy gain, and body condition in animals (McNamara & Houston, 1994). However, outside of measures of activity, little is known regarding personality trait expression and measures of an individual's physical condition.

Euprymna tasmanica (Pfeffer, 1884), the southern dumpling squid, is an excellent invertebrate species with which to study the relationship between personality, biology, and resulting life history in animals. *Euprymna tasmanica* is a small (~4–7 cm), relatively solitary, benthic squid with complex behavior and a short life span (5–8 months). Unlike true squid (order: Teuthida), dumpling squid (order: Sepiolida) do not school but spend their lives associated with soft substratum, burying into sand or mud during daylight hours and emerging at night to "sit" on the bottom to feed. They can be held individually in the laboratory under seminatural conditions while maintaining their normal range of behaviors. Cephalopods have highly variable and complex life history traits related to growth and reproduction; these factors are particularly sensitive to environmental conditions (Boyle, Pierce, & Hastie, 1995; Moltshaniwskyj, 1995). Little is known about how behavior mediates these relationships in squid and contributes to fitness-related outcomes, especially reproduction and survival. From a comparative psychological standpoint, cephalopods are invertebrates that potentially display similar psychological characteristics to vertebrates (Mather & Anderson, 1993; Sinn et al., 2001). Understanding the processes by which these similarities have arisen, both proximate and ultimate, should be informative of the evolution of personality itself.

In summary, the three major aims of this study were as follows: (a) to examine whether observable, discrete behaviors in a sepiolid squid could be reliably grouped to describe personality traits; (b) to assess whether these traits were expressed in a domain-general or context-specific manner; and (c) to examine the relationship be-

tween personality trait expression and several biological measures: sex, maturity stage, body size, reproductive condition, and somatic condition.

Method

Subjects

Dumpling squid (*Euprymna tasmanica*) were collected from a wild population on four different occasions at Kelso, Tasmania (41° 06'S by 146° 47'E), by snorkel or scuba, between February 16, 2002, and June 6, 2002. All squid (including those that were partially buried) encountered during dives were collected, with the exception of obvious juveniles (< 1 cm mantle length [ML]). Squid were transported to the University of Tasmania, Launceston, Tasmania, Australia, and held in separate plastic test containers (34 cm long × 29 cm wide × 13 cm deep) floating in a larger 2,000-L recirculating seawater system. Of the 97 mature adults used in this study, 33 were females and 64 were males. Mean ML and wet weight (WW) of subjects ($N = 97$) was 24.2 mm ($SD = 5.41$) and 6.09 g ($SD = 5.25$), respectively. Seawater was maintained at 33–34 ppt and 18 °C. Individual test containers were opaque on all sides and contained a thin layer (3–4 mm) of sand, allowing squid to partially bury themselves while being visible to an observer. The system received overhead lighting maintained on a 14:10-hr day–night cycle and was continuously illuminated with low levels of red light (0.22×10^{14} quanta $s^{-1}cm^{-2}$) to allow for visual observation during nighttime hours. After capture, squid were allowed to acclimate for 48 hr and were then fed once (mysid shrimp: *Tasmanomysis oculata* and *Paramesopodopsis rufa*) and given another 48 hr before testing began. Maintenance and growth rations of mysid shrimp for dumpling squid have been determined previously (Fox-Smith, 2002), and feeding during the present study met or exceeded growth rations. During acclimatization and experimentation, human interaction with squid was minimized through the use of visual barriers surrounding the experimental system. At the end of testing, squid were euthanized by chilling (Anderson, 1996) and then were frozen. Within 72 hr of freezing, squid were thawed and the following parameters were measured: gender, ML (distance from center of eye to distal portion of mantle; see Figure 1A), total WW, and gonad complex weight (GW).

Behavioral Test Procedures

Six to 12 hr before testing, all test containers were covered with opaque plastic lids, which allowed for testing of each squid without disturbing neighboring individuals. All testing began 1–2 hr after the start of the dark phase in the laboratory. All squid were subject to two tests on each testing day, with each test designed to simulate a different ecological context. The first test was a threat, in which the experimenter (DLS) lifted the lid of the test container and touched the squid on its arms with one end of a 50-ml plastic eyedropper that was moved toward the subject at approximately 3 cm/s. The end of the plastic eyedropper was colored to enhance visual acuity. Squid were touched until they moved away from the threat or up to 10 times, whichever came first. Behaviors were recorded for 5 min from the time of movement from the threat or the 10th touch. The second test was a feeding event that occurred 60–90 min after the threat test and consisted of the experimenter presenting live food (25–35 mysid shrimp). Shrimp were placed in the corner of the test container farthest from the squid; when squid were located centrally, shrimp were placed in the right-hand corner of the test container closest to the observer. Behaviors in this test were recorded for 5 min or until the capture of five prey items. Frequency and duration of behaviors were recorded with an audiocassette recorder and handheld timer. An a priori 5-s rule was used for all frequency counts, in which a behavior was scored as a multiple frequency only if there was at least a 5-s break between occurrences. The variable *feeding distance* was measured from feeding strikes filmed during testing with a

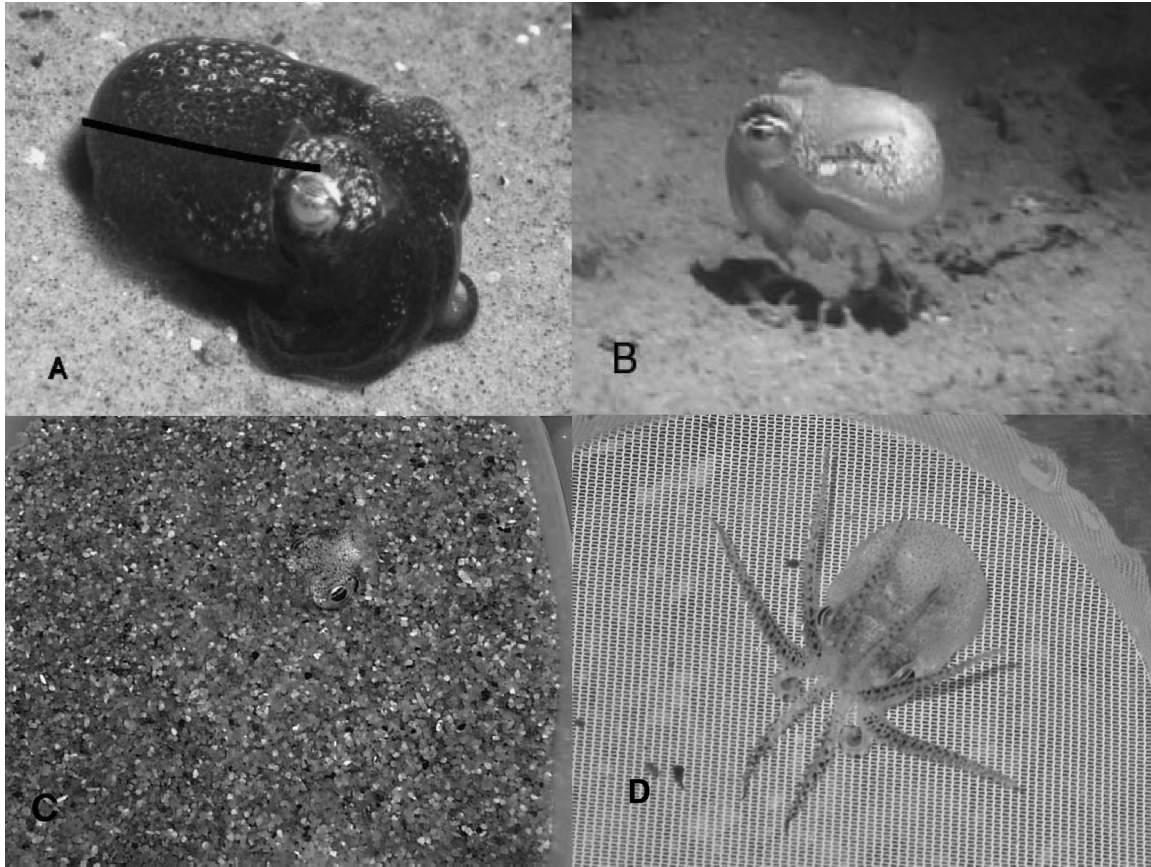


Figure 1. The southern dumpling squid, *Euprymna tasmanica*. A: In a sitting position atop sand substrate. Black line indicates mantle length measurement. B: In the wild at Kelso, Tasmania, using mantle fins to swim in a stationary position in the water column (i.e., the behavior *fin swim*). C: Partially buried in sand substrate. D: Arm flower posture. Photo credits: David Mitchell (A), John Forsythe (B), Mike Steer (C), and Rebecca van Gelderen (D).

Sony digital video camera (DCR-TRV900E). Squid were normally sitting on the sand substrate when a feeding strike began; to capture a mysid, the squid swam to the prey, performed a tentacular strike, and then returned to the bottom substrate. The distance from the sitting position to the tentacular strike was defined as the feeding distance; a ruler on the side of the test container provided a scale for measurements.

Each squid was tested twice weekly for 2 weeks. Within a given week, squid were given both tests on 2 different days separated by at least 48 hr. Although the order of tests remained the same (i.e., threat first, then feed), squid were tested in a different order each test day. In order to increase the between-individuals variance in our behavioral measures and to account for within-individual variability (Fleeson, 2004), data from the two threat periods within a week were combined for analysis; the same procedure was applied to feed test observations. Combined frequencies and times from the first week of testing were used to define potential personality traits. Combined results from the second week of testing were used for test–retest comparisons.

Data Analysis: Aims 1 and 2

Principal components analysis (PCA) and reliability and stability measurements on PCA data were used to address the first aim of our study: Can observable behaviors in squid be reliably grouped to reflect behavioral styles or personality traits? PCA scores were used to address our second

aim: Are personality traits expressed in squid in a context-specific or in a domain-general manner?

Twelve behaviors were recorded during threat testing and were used in our analysis to define possible personality trait dimensions (see Table 1). A categorical variable (*first behavior after touch*) describing the squid's first reaction to the threat stimulus was included in the threat analysis. This variable ranged from 1 to 9. Lower numbers indicated a more shy or reactive response, whereas on the opposite end of the scale an individual's reaction would have been more bold and aggressive and less reactive: 1 = *jet*, 2 = *fin swim*, 3 = *amble*, 4 = *ink*, 5 = *bury*, 6 = *no reaction*, 7 = *color change*, 8 = *arm flower posture*, and 9 = *grab*. Eleven behaviors were recorded during feed testing (see Table 1). Variables from both tests were screened for distributional characteristics and intercorrelations. The time variables *time to first feed* and *time to first bury blow* reflected latency scores; a squid received a 300 (i.e., 300 s or 5 min) for this variable if it did not perform either of these behaviors in a given test. Both variables were also log transformed to approximate normal distributions. No other transformations were necessary.

Data from each test were analyzed by using SPSS Version 10.0 to conduct a PCA with Varimax rotation (Tabachnick & Fidell, 1996). Orthogonal rotation was chosen on empirical grounds, as it allowed a unique set of scores to be generated from the data set. Oblique rotation was performed as well and produced the same outcome as the orthogonal methods for each analysis. The number of components interpreted for each

Table 1

Definitions of Behaviors Measured in Threat and Feeding Tests and Used in Principal Components Analysis (N = 97)

Behavior	Threat		Feeding		Operational definition and type of variable
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	
Bury blow	2.86	3.33	0.36	0.88	Squid attempts to bury, by directing water blasts through the funnel into the sand substrate (frequency count).
Color change	1.88	2.41	Not included		At least 50% of squid's overall skin color pattern changes (frequency count).
Jet	1.46	1.07	0.14	0.46	Squid moves by jet propulsion, with no contact to the bottom or sides of the container (frequency count).
Arm flower posture	0.62	1.45	Not included		Squid spreads all the arms out, with ventral suckers facing the direction of the stimulus (Figure 1D). Performed while swimming or stationary (frequency count).
Number of touches	6.57	6.29	Did not occur		Number of times that threat eyedropper touches squid before the squid moves away (frequency count).
Time spent moving	27.24	33.09	7.28	28.62	Total time squid moves during testing. This includes time spent ambling, fin swimming, and jetting (s).
Ink	2.19	2.98	0.23	1.93	Squid ejects ink blob into water column (frequency count).
Amble	2.79	3.05	0.45	0.93	Squid moves across test container while maintaining contact with the arms on the bottom substrate (frequency count).
Fin swim	0.76	1.72	0.31	1.06	Squid hovers in the water column while using the mantle fins to maintain position (frequency count).
Grab	1.32	3.03	Did not occur		Squid uses more than one arm to initiate contact with the threat stimulus (frequency count).
First behavior after touch	6.50	5.26	Did not occur		The first behavior that occurred after the threat eyedropper contacts squid (categorical variable).
Time to first bury blow	468.74	139.60	537.75	131.36	Time elapsed from the start of the test until the first bury blow was recorded (s).
Number of feeding strikes	Did not occur		4.61	4.17	Number of times the squid captured prey item (frequency count).
Average feeding distance	Did not occur		25.18	24.36	Average distance traveled to capture prey item (mm).
Time to first feeding strike	Did not occur		391.18	194.99	Time elapsed from the start of testing until squid captured its first prey item (s).
Feeding rate	Did not occur		235.04	288.11	Total time spent feeding divided by the total number of feeding strikes (s/number of strikes).

analysis was based on (a) a scree test (Cattell, 1966), (b) a parallel analysis (Montanelli & Humphreys, 1976), and (c) interpretability of the components themselves (Zwick & Velicer, 1986). For component interpretation, behaviors with a loading of at least $\pm .32$ were considered to contribute to the meaning of a component (Tabachnick & Fidell, 1996). A regression method, which results in the highest correlations between components and component scores (Tabachnick & Fidell, 1996), was used to compute scores for both PCA solutions. For example, to calculate a threat reactivity score for Week 1, all frequency counts and time measurements of behaviors from Week 1 were multiplied by their respective PCA loadings for the component *threat reactivity* (see Table 2) and added together to create a regression score. In this way, behaviors that contributed the most to the meaning of a component (i.e., high loadings equal high regression coefficients) also contributed the most to an individual's score on that trait. Thus, at the end of our PCAs on Week 1 data, we had two solution matrices, one per test situation, with unique component scores for each individual squid for each trait measured.

To assess the consistency of trait expression levels across time, a PCA was run for each test with the data obtained from Week 2 observations and scores were generated as described for Week 1. One-way random effects intraclass correlation coefficients (hereafter referred to as *repeatability*; e.g., Sokal & Rohlf, 1995) were computed to measure consistency and agreement of individual scores between the test (Week 1) and retest (Week 2) results ($n = 71$). Repeatability is a measure of change in trait expression of individuals across time, relative to the change of the study population. Values approaching 1 indicate that relative change of individuals is low, whereas values approaching 0 indicate that within-individual variance is high relative to the group (Falconer & Mackay, 1996; Lessells & Boag,

1987). Convergent and divergent stability, both of the Week 1 results and across Weeks 1 and 2, was also examined to assess the validity of our personality measures (see the Appendix).

To examine whether traits were expressed in a context-specific or domain-general manner, Pearson correlations between threat component scores and feed component scores were calculated. If personality traits were domain-general, then component scores with similar meanings from each test should be correlated across test scenarios. If scores for traits having the same meaning but derived from the two tests were not correlated, then this would indicate context-specific trait expression.

Aim 3: Correlates Between Personality Traits and Biological Parameters

Sex and maturity stage. The relationship between gender and maturity stage on the variability in personality scores from the PCA solutions was assessed with a two-way multivariate analysis of variance (Tabachnick & Fidell, 1996) and SPSS 10.0 ($n = 71$). Eight continuous personality trait measures (traits were context-specific; see Results) were entered into the model as dependent variables, whereas sex (two levels: male and female) and maturity stage (three levels: immature, maturing, and mature) were the independent variables. The reproductive maturity stage of individual squid was classified according to Lipinski (1979) on the basis of the size and structure of the reproductive organs. Canonical discriminant analysis was used post hoc to examine any significant interactions or main effects from this model (Tabachnick & Fidell, 1996). All continuous variables satisfied the criterion of normality and bivariate linearity.

Table 2
Component Loadings of Behaviors Observed During Threat Tests on Four Orthogonally Rotated Principal Components (N = 97)

Behavior	Principal component			
	Shy avoidance–bold aggression	Activity	Bury persistence	Reactivity
Number of touches	.802	–.201	–.095	–.338
First behavior after touch	.864	.111	.001	–.282
Jet	–.638	.150	–.134	.562
Grab	.845	.000	–.043	.140
Arm flower posture	.424	.683	–.174	.264
Log time spent moving	–.434	.684	.366	.019
Amble	–.128	.569	.613	–.326
Color change	–.032	.561	.143	–.089
Fin swim	–.037	.863	–.047	–.051
Log time to first bury	–.023	–.035	–.859	–.171
Bury	–.038	.057	.941	–.017
Ink	–.210	–.140	.129	.823
% variance explained	29.3	22.6	14.4	8.8
% total variance	75.1			

Note. Boldface indicates the highest component loading(s) for each behavior.

Body size and somatic and reproductive condition. Pearson correlations between personality trait scores and two measures of body size—ML and WW—were used to examine the relationship of body size on trait expression levels ($n = 71$). A Bonferroni-corrected Type I p value of .003 was used as our cutoff to indicate a significant correlation.

Size-independent measures of somatic and reproductive condition were obtained as residuals from regression analysis (Garcia-Berthou, 2001). Somatic condition was a studentized residual (difference between observed and predicted values) from a regression of log ML versus log WW ($n = 88$; see Figure 2). Individuals with positive residuals would be in better somatic

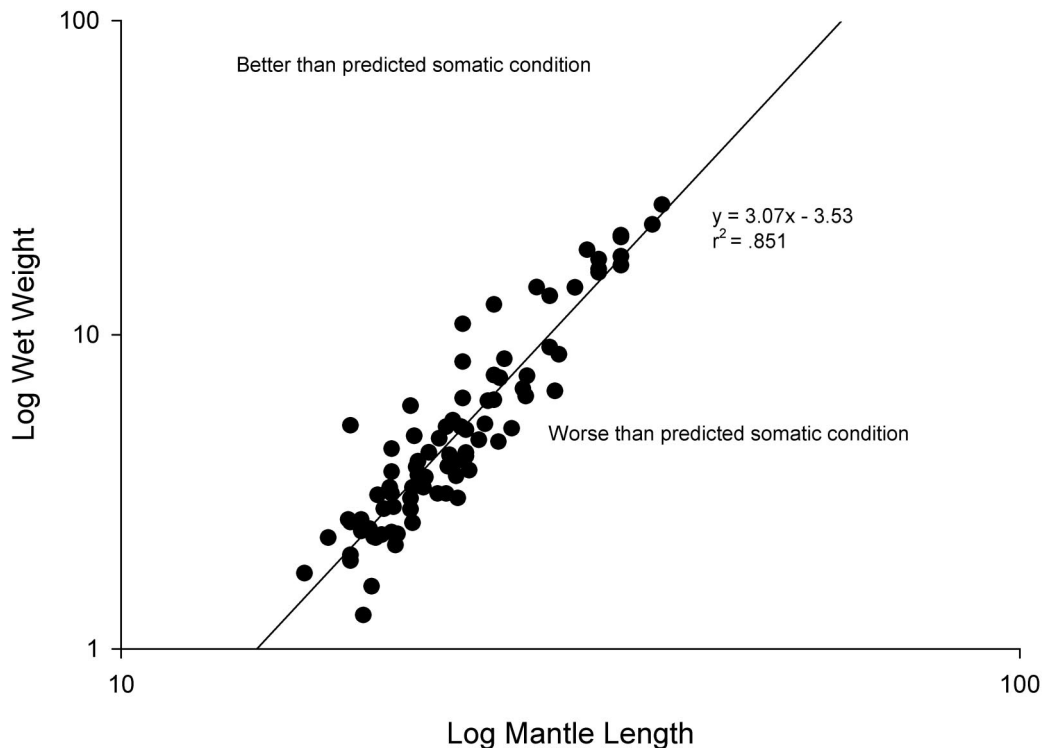


Figure 2. Calculating somatic condition in dumpling squid ($n = 88$). A least squares regression between log mantle length (mm) and log wet weight (g) provided a predicted value for each point. Studentized residuals measured the deviance from a predicted weight, given a particular size, for each individual.

condition (heavier) than individuals with negative residuals. In the case of reproductive condition, a regression of GW versus WW was used ($n = 71$). Squid allocating more energy toward reproduction could be expected to have positive residuals, whereas animals with a lower reproductive condition would have negative residuals. For both regression equations, the slopes for males and females were compared by means of t tests (Zar, 1984). If the slopes of the lines were not different, residuals were calculated from a regression using all individuals. Conversely, if the slopes were different, then residuals from the sex-specific lines were used for residual calculations. Studentized residuals of condition were then entered into two regression equations (Tabachnick & Fidell, 1996) with the eight personality trait scores ($n = 62$); the first equation used somatic condition as the dependent variable, and the second equation used reproductive condition as the dependent variable. All variables in this analysis were first screened for distributional properties and bivariate linearity. SPSS 10.0 for Windows was used in all correlation, residual computation, and regression calculations.

Results

Aims 1 and 2: Defining Personality Traits and Assessing Their Expression Structure and Reliability

Four components from the PCAs were chosen as a best fit of the data (75.2% of the variance accounted for in the threat test [see Table 2]; 78.4% of the variance accounted for in the feed test [see Table 3]). The component names *shy avoidance–bold aggression*, *activity*, *reactivity*, and *bury persistence* were chosen in both test situations to describe behaviors that loaded highly on each component in each PCA solution (see Tables 2 and 3). Thus, squid that had higher scores on the shy avoidance–bold aggression component in the threat test moved only after multiple touches with the eyedropper, grabbed or performed arm flowers (see Figure 1D) toward the stimulus, and moved for less time but not by jetting away. Squid at the opposite end of this continuum jetted away from the eyedropper after fewer touches, spent more time moving away, and did not grab the threat or perform arm flowers toward it. Similarly, the continuum of shy avoidance–bold aggression in the feeding context described differences among individuals in the

number of feeding strikes, distance traveled to feed, handling time of food, and time to first feeding response. An increase in the number of feeding strikes and distance traveled, a quicker response to the first food item, and less time spent per item described bolder or more aggressive individuals in this test (a lower PCA score due to the sign of loadings). Shyer, less aggressive individuals in the feed test took longer to feed, did not feed as quickly or as much, and traveled shorter distances to do so (a higher PCA score). Active squid in both tests spent more time moving by ambling and fin swimming than did less active individuals. More reactive squid jetted and inked more than did less reactive individuals and in the threat test, performed these behaviors after fewer touches with the stimulus.

Week 2 PCA solutions from the threat and feed tests produced solutions with identical meaning to that obtained during Week 1 (for empirical measures of this association, see Appendix). Similar amounts of variation were also explained by the four component solutions from Week 2 (79% variance for threat test; 72% variance for feed test). There was also a high degree of within-individual consistency for six personality traits between the two test weeks. For threat tests, repeatability for shy avoidance–bold aggression was $\rho = .68$, $F(70, 71) = 3.10$, $p < .001$; for activity, $\rho = .57$, $F(70, 71) = 2.35$, $p < .001$; and for reactivity, $\rho = .63$, $F(70, 71) = 2.68$, $p < .001$. Week 1 to Week 2 feed test repeatabilities for shy avoidance–bold aggression were $\rho = .54$, $F(70, 71) = 2.20$, $p < .001$; for activity, $\rho = .43$, $F(70, 71) = 1.75$, $p < .05$; and for reactivity, $\rho = .39$, $F(70, 71) = 1.64$, $p < .05$. Bury persistence repeatabilities were lower than the other trait measurements within each context, indicating less consistency in this measure: For the threat test, repeatability was $\rho = .19$, $F(70, 71) = 1.24$, $p = .20$; for the feed test, $\rho = .33$, $F(70, 71) = 1.49$, $p < .001$. These results, along with our convergent and divergent stability analyses (see the Appendix), suggest that the PCA solutions were measuring consistent aspects of personality.

With the exception of bury persistence ($r = .35$, $p < .001$), correlations within trait but across tests generated from the Week

Table 3
Component Loadings of Behaviors Observed During Feed Tests on Four Orthogonally Rotated Principal Components (N = 97)

Behavior	Principal component			
	Shy avoidance–bold aggression	Activity	Bury persistence	Reactivity
Time to first feeding strike	.932	–.115	.040	–.022
Number of feeding strikes	–.963	.071	.034	.043
Average distance traveled	–.880	–.078	.010	–.011
Feeding rate	.937	–.070	.011	.006
Amble	–.044	.809	–.008	–.324
Fin swim	–.026	.661	–.006	.335
Log time spent moving	–.069	.911	.010	.228
Bury	.095	.016	.901	.136
Log time to first bury	.104	.018	–.886	.051
Jet	–.194	.149	–.149	.794
Ink	.150	.030	.253	.708
% variance explained	32.8	18.7	15.6	11.3
% total variance	78.4			

Note. Boldface indicates the highest component loading(s) for each behavior.

1 data were weak (.090–.196) and not significant (see Table 4). For Week 2 data, traits were again context-specific, with no within-trait across-context correlation greater than .28 (for shy avoidance–bold aggression). Therefore, trait expression levels in our tests, as measured by PCA scores, were not correlated and thus were expressed in a context-specific manner.

Aim 3: Are There Biological Correlates of Squid Personality Traits?

Sex and maturity stage. A two-way multivariate analysis of variance indicated a significant difference in the suite of trait scores dependent on maturity stage, Pillai's trace(16, 118) = .420, $p < .05$, but not on sex, Pillai's trace(8, 58) = .166, $p = .20$, or a Sex \times Maturity Stage interaction, Pillai's trace(16, 118) = .307, $p = .19$. The canonical discriminant analysis indicated the importance of two personality trait groupings in discriminating between maturity stages (see Figure 3). Fully mature squid were more threat active, threat bold, and less feed reactive in our sample. Maturing and fully mature squid were also less feeding bold and more threat reactive than immature squid.

Body size and somatic and reproductive condition. Univariate correlations between our two measures of body size (ML and WW) and eight personality trait scores yielded one significant correlation. Shyer or more avoidant squid in the feed test—that is, those that fed fewer times, took longer to take the first feeding strike, traveled less distance to do so, and handled food longer—were larger ($r = .36$, $n = 88$, $p = .001$). All other correlations between the personality traits and measures of body size were small and not significant.

No significant difference between slopes of lines for sexes was found for the relationship between ML and WW. Thus, residual scores for our somatic index are based on a sex-independent prediction line, $R^2 = .851$, $F(1, 87) = 490.4$, $p < .001$. For the relationship WW versus GW, a significant difference was found between sex-specific regression lines, $t(66) = 25.9$, $p < .05$. Thus, two separate regression equations were used to compute residuals for our reproductive index, one for each sex: for females, $R^2 = .416$, $F(1, 27) = 18.51$, $p < .001$; for males, $R^2 = .886$, $F(1, 42) = 319.65$, $p < .001$. The results from the two regression equations between the set of behavioral variables (eight PCA personality trait scores, four from each test scenario) and the biological indices (one somatic and one reproductive) were nonsignificant, indicating that there was not a relationship in our sample between an indi-

vidual's personality expression and its current somatic or reproductive condition: for somatic condition, $R^2 = .130$, $F(8, 79) = 1.48$, $p = .179$; for reproductive condition, $R^2 = .107$, $F(8, 62) = 0.925$, $p = .502$.

Discussion

Trait Interpretation and Structure

Squid reacted to tests in a very individualized manner. Extremely reactive squid were immediately apparent, as they jetted and inked numerous times from stimuli. In threat tests, some acted boldly or aggressively, grabbing, performing arm flowers, or ignoring the stimulus. Shy or avoidant squid in threat tests moved away from the stimulus, usually after only one or two touches. Feeding differences were apparent as well, with bold individuals feeding quickly and over long distances; others were shyer, taking short-distance feeding strikes interspersed over longer time. Of course, there was a wide range of intermediate individuals in both tests that reacted to stimuli but did not do so in such an extreme manner. The naming of our components, although subjective, captured the essence of these aggregate behaviors in squid. PCA results, an objective measure of these aggregates, were stable and allowed characterization of behavioral continuums in our sample through the use of PCA scores.

With the exception of bury persistence, our measures of repeatability of threat traits were high (.59–.67) and, along with the convergent and divergent measures over time (see the Appendix), indicate that personality traits in threatening situations for squid were reliable. Our feed test repeatabilities were lower (.38–.54) but perhaps reflect differences in plasticity, learning, or both in feed personality traits. Repeatabilities in this study were measured over a 1-week period. Given that the life span of a dumpling squid can be as short as 20 weeks, this period represented close to 5% of its total life, an equivalent of approximately 4 years in a long-lived primate. Testing over longer time periods for short-lived species can confound interpretations of repeatabilities because of processes of maturation and development. Consistent trait variation between individuals is an essential component of selection regimes (Endler, 1986), and the repeatability measures in this study satisfy the criterion of measuring consistency within individuals relative to the study population as a whole (Fleeson, 2004; Lyons et al., 1988).

Table 4
Pearson Correlations Between Four Personality Traits Measured for Dumpling Squid in a Threat and a Feeding Test (N = 97)

Personality trait (feeding test)	Threat test			
	Shy avoidance–bold aggression	Activity	Reactivity	Bury persistence
Shy avoidance–bold aggression	.196	.003	.128	–.136
Activity	–.076	.090	–.006	.090
Reactivity	–.066	–.155	.162	.218
Bury persistence	.212	–.103	.318	.354

Note. Boldface indicates within-trait across-test correlations.

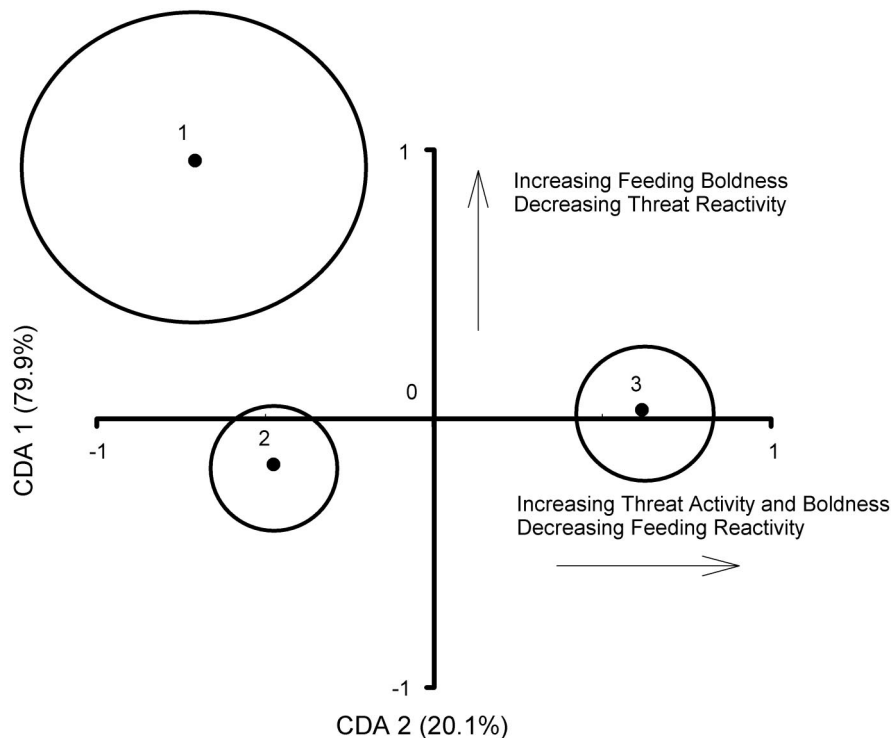


Figure 3. Post hoc canonical discriminant analysis from significant interaction between squid maturity stage and personality traits ($n = 71$). Circles represent 95% confidence intervals for maturity stage group centroids (1 = immature, 2 = maturing, and 3 = mature). Percentage of variance explained by each discriminant function is given in axis parentheses. CDA = canonical discriminant axis.

Our results indicate that for the southern dumpling squid, personality trait expression is context-specific, at least within the scenarios of a threat and a feeding test. This was indicated by the low within-trait across-context correlations, and this relationship was maintained for both weeks of testing. Thus, active squid in the threat test were not necessarily active in our feeding one. This was also the case for the other three traits under study. From an ecological standpoint, every important situation that affects survival and reproduction potentially requires a different adaptive response (Coleman & Wilson, 1998). However, domain-generality also appears to be widespread (Sih et al., 2004). The notion of domain-generality implies limited behavioral plasticity, which can arise if selection drives a trait in the same direction across contexts or if traits are constrained through genetic relationships (Falconer & Mackay, 1996). It is evident that selection has resulted in both context-specific (mammals: Reale et al., 2000; Seaman, Davidson, & Waran, 2002; reptiles: Yang, Phelps, Crews, & Wilczynski, 2001; fishes: Coleman & Wilson, 1998) and domain-general (mammals: Kooij et al., 2002; Lyons et al., 1988; Visser et al., 2001; fishes: Huntingford, 1982; Ward et al., 2004) personality trait structure in animals. Further research is needed to determine what ecological (i.e., social systems, habitat, phylogeny, etc.) and psychological (i.e., trait type and context and genetic bases) patterns have resulted in particular personality trait structures. The current results reinforce the need for researchers to explicitly examine context-specific versus domain-general trait expression instead of assuming one or the other (Sih et al., 2004).

Biological Correlates

Sex and somatic and reproductive condition did not explain significant personality trait variation in squid. However, fully mature squid were more active and bold in threatening situations, while also being less reactive in feeding situations. Likewise, there was a decrease in feeding boldness and an increase in threat reactivity measures in more mature squid. Reproductive maturity, and its associated metabolic costs, should be reflected in an individual's behavioral approach to situations involving survival, because of the influence of energetic state on decisions regarding feeding and predation risk (Aeschlimann, Haeberli, & Milinski, 2000). The increases that we observed in boldness and activity for sexually mature squid in the face of threatening scenarios may indicate a need to increase foraging rates because of increased metabolic demands as well as a need to find potential mates. For both sexes, finding mates and encountering food during the last few weeks of life are critical because mating and egg laying in sepiolid squid occur over a period of 2–3 weeks prior to death (Steer, Moltshaniwskyj, Nichols, & Miller, 2004). If the benefits of increased activity and boldness during this life stage in squid outweigh the costs of increased encounter rates with predators (Werner & Anholt, 1993), then becoming more active and bold may be an adaptive strategy for squid that are ready to reproduce. Becoming more willing to flee from lethal encounters (higher threat reactivity) and less likely to jet away and leave potential food sources (lower feed reactivity) may also complement survival strategies under increased activity levels, if increased movement

increases predator interaction. This pattern of increasing threat boldness with increasing maturity has been demonstrated in another marine mollusk, the common whelk (Rochette et al., 2001), and these results fit well with foraging behavior and predator avoidance theory (Lima & Dill, 1990).

An interesting result of this study was the link between larger, more mature squid and increased levels of feeding shyness. Increased boldness is correlated with body size in fish (Magnhagen & Staffan, 2003) and may result in increased growth (Sundström et al., 2004; Ward et al., 2004). Body size also has consequences for an individual's survival and fitness (Quinn & Peterson, 1996; Werner & Gilliam, 1984), explaining why larger bold feeders are observed in some populations. However, there are costs as well as benefits associated with being larger and bolder. Bolder individuals feeding first and more often may also suffer greater mortality because of increased exposure to predation (Johnsson, 1993), thus allowing the maintenance of shy strategies in populations. Furthermore, social systems may help explain the observed patterns of shyness and body size in squid. Little is known about shy–bold feeding strategies in nonsocial species, such as sepiolid squid. Dominance hierarchies are prominent in those species exhibiting increasing boldness with increasing body size (Huntingford, Metcalfe, Thorpe, Graham, & Adams, 1990; Sneddon, 2003; Ward et al., 2004). Sepiolid squid form loose aggregations in the field, but their social systems most likely lack feeding dominance hierarchies (Boal, 1996; but see Mather, 1986). Species that do not exhibit strong social ties then may have differing patterns of feeding boldness and body size. Higher metabolic costs and predation risks associated with bolder feeding approaches may help explain why shyer feeding squid were larger in our sample. Further work is needed on the relationship between the life history of nongregarious species and adult behavioral outcomes, a relationship that has received some attention in some schooling fishes (Rodd, Reznick, & Sokolowski, 1997).

The absence of correlations between squid personality traits and somatic and reproductive status may be a function of flexible strategies of somatic and reproductive energy allocation in squid (Boyle & von Boletzky, 1996; Pecl, 2001). Squid are able to quickly (on the order of weeks) adjust energy allocation and growth rates according to changing ambient conditions, such as temperature and day length (McGrath Steer & Jackson, 2004). Thus, we interpret this aspect of our results with caution. Further studies incorporating time and ration effects are needed to understand the relationship between personality and condition indices in animals.

Evidence for Convergence Across Cephalopod Studies and Activity as a Dimension of Personality

Three of the personality traits in our study could be broadly interpreted as shy avoidance–bold aggression, activity, and reactivity and represent major axes of variation witnessed across many animal taxa (Gosling, 2001; Sih et al., 2004). The final trait, bury persistence, may be a species-specific trait or may have resulted from our test procedures (squid could not bury completely, so they tried to bury more or less often, depending on the individual). For our first principal component, we chose to use the terminology of *shy avoidance–bold aggression* to denote that our tests could not discriminate between these two traits. This component in our study

is defined by behaviors that could be interpreted as either aggressive, shy–bold, or both. Most studies treat these traits separately (e.g., Bakker, 1986; Forkman, Furuhaug, & Jensen, 1995; Wilson, Coleman, Clark, & Biederman, 1993), whereas other studies choose a trait dimension name that could encompass the meaning of both traits (e.g., Fairbanks, 2001). Several studies have found that aggressiveness is correlated with boldness (Huntingford, 1982; Riechert & Hedrick, 1993), and both traits also appear to be linked ecologically and psychologically in sepiolid squid. Further tests should determine whether these traits are indeed linked in squid or whether they form meaningfully different traits, as they do in octopuses (Sinn et al., 2001).

This is the third study on temperament or personality among the coleoid cephalopods that has identified activity as a trait dimension (see also Mather & Anderson, 1993; Sinn et al., 2001). The identification of this trait across three different studies, in addition to its low correlates with shy–bold measures (the present study and Sinn et al., 2001), leads us to believe not only that activity is a personality dimension in cephalopods but that it is separate from an individual's willingness to take risks, or its boldness. Activity is a simple and straightforward measure that is important for survival, growth, and dispersal (Werner & Anholt, 1993). However, many researchers implicitly subsume activity (and sometimes reactivity) under the trait construct shy–bold (e.g., Bell, 2004; Sneddon, 2003) or *exploratory behavior* (e.g., Dingemanse, Both, van Noordwijk, Rutten, & Drent, 2003), and its utility in direct comparisons between animal personality traits and the human Big Five factors (McCrae & Costa, 1999) is weak (Gosling & John, 1999). Notably, in both human and nonhuman primate temperament research (i.e., juvenile studies), activity is considered a major axis of variation (Byrne & Suomi, 1995; Kagan, 2003). However, the role of activity in explaining adult primate variation is greatly diminished, as it is thought to become only a component of adult extraversion (A. Buss, 1989). Is activity an important behavioral trait for some taxa and life stages (e.g., invertebrates, reptiles, and juvenile vertebrates) but not for others (e.g., adult primates, including humans)? Is it truly a lower order trait subsumed under a higher order shy–bold substrate within some animals' psychological makeup (i.e., birds and fishes) but not in others' (i.e., invertebrates and reptiles)?

Conclusion

Given the reliability of trait measures in this study, the convergence across cephalopod studies, and the links between personality traits and biological parameters in squid, we conclude that quantifying personality traits in cephalopods can be done with the same reliability as what is normally considered for higher vertebrates. Further studies on invertebrate personality structure and function should continue to contribute to our knowledge of evolutionary origins and patterns of personality traits across phylogeny.

A central tool for formulating hypotheses about the significance or function of any trait is examining its morphological, physiological, ecological, environmental, or other correlates (Hayes & Jenkins, 1997). This study begins to illustrate potential correlates in squid, and these results illustrate how integrating personality trait expression with an individual's biology may be useful toward understanding the interplay of behavior and life history strategies. Comparative studies have already begun to illustrate the relation-

ship between personality and an individual's survival and fitness (i.e., boldness: Cavigelli & McClintock, 2003; Godin & Dugatkin, 1996; activity or exploration: Dingemanse, Both, Drent, & Tinbergen, 2004), and the current results illustrate further areas of research in squid and other animals that may be fruitful toward understanding personality traits and fitness-related consequences. In our opinion, this is the ultimate utility of nonhuman personality study, as comparative studies are especially well suited to providing information as to how continuous behavioral variation and natural selection interact (Endler, 2000) and the resulting influence of personality on population dynamics (Biro, Post, & Parkinson, 2003; Mougeot, Redpath, Leckie, & Hudson, 2003).

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Appendix

Reliability and Stability of Squid Personality Traits

Because of the lack of studies on personality traits in invertebrates and a perceived reluctance for researchers to designate trait construct terms such as personality to other nonhuman animals (for an example with rats, see Karli, 1989), we undertook a number of additional assessments of our PCA solutions in order to satisfy, at least on an empirical level, assumptions generally held by personality psychologists concerning the validity of their trait measurements.

Internal consistencies of trait scores are an important issue for studies using questionnaire methods (e.g., Gosling, 1998). However, for PCA models with orthogonal rotation, component scores are exact, and thus, measures of internal consistency (such as squared multiple correlations of component scores predicted from scores on observed variables or Cronbach's alpha) are either uninformative (in the first case, squared multiple correlations are 1—a completely exact result; Tabachnick & Fidell, 1996) or inappropriate (Cronbach's alpha was designed for questionnaire methods). Therefore, no measures of internal consistency of component scores are reported here.

Convergent and divergent stability of trait dimensions was assessed in three ways. First, the similarity of solution matrices obtained through differing methods of rotation (oblique vs. orthogonal) on Week 1 results were used to assess convergent validity of the component structure. Second, communalities of variables and magnitude of variable loadings obtained during PCA from Week 1 were used to assess the strength of the relationships of the variables in our PCA solution. Third, longitudinal convergence and divergence were assessed by comparison of the Week 1 component solutions ($N = 97$) and the component solutions obtained from PCAs performed on Week 2 data ($n = 71$). For the longitudinal assessment, component loadings from both threat and feed solution matrices from both weeks were first normalized with Fisher's r -to- z ratio (Snedecor & Cochran, 1980) and then entered into a new data set (Variables \times Components at each test time). Pearson correlations (two-tailed) were then computed ($N = 12$ for the threat test; $N = 11$ for the feed test) with the normalized component loadings across the test situations and time points. Convergent reliability for PCA solution matrices was assessed by high correlations within the same trait dimensions at different time points; divergent reliability was assessed within tests through relatively lower correlations between different dimensions at different time points.

For Week 1, the threat-test-only solution matrix, communalities of all variables were greater than .74 (with the exception of color change, which

was .34) and all behaviors had a loading greater than .56 on one of the components. Only one discrepancy was found between orthogonal and oblique rotation methods in the Week 1 threat-test solution matrix. Instead of loading on both the shy avoidance–bold aggression and reactivity components, the variable *number of touches* loaded only onto the shy avoidance–bold aggression component in an oblique solution (but loadings of this behavior between the two rotation methods differed by an absolute value of .084). Correlations between components under an oblique rotation were small (.036–.155), reinforcing our decision to use an orthogonal rotation for statistical reasons. The feed-test-only solution exhibited similar characteristics of convergent stability, with all communalities above .55 and all behaviors loading above .66 on at least one component. A comparison of oblique versus orthogonal rotation of the feed test results at Week 1 yielded similar invariance, with only a single discrepancy between the two types of rotation (fin swim did not load on reactivity in the oblique solution). Correlations between obliquely rotated components were again small (.012–.132).

To assess trait convergence and divergence over time, the normalized component loadings from Week 1 solution matrices were correlated with the normalized component loadings from the Week 2 solution matrices. As in multitrait–multimethod correlations, the correlation between the same components across time is expected to exceed the correlations across different components. For the threat solutions, correlations within components across time were high (.73–.95); three out of four within-trait correlations were significant (Bonferroni-adjusted $\alpha = .003$). In addition, correlations between different components across time were consistently lower (.10–.55), and all were nonsignificant. For the feed solutions, the four within-component correlations across time were all higher (.88–.98) than the between-components correlations (.012–.27). Within-component correlations for the feed test all reached significance ($p < .001$), whereas all across-components correlations were nonsignificant. The strength of the loading patterns for the variables in our PCAs, coupled with the high convergent and divergent stability of solution matrices across time, was indicative of the strength of assessing personality trait expression in squid through the use of discrete, observable behaviors.

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